

Natal dispersal patterns are not associated with inbreeding avoidance in the Seychelles warbler

C. EIKENAAR,* J. KOMDEUR* & D. S. RICHARDSON†

*Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Haren, The Netherlands

†Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, UK

Keywords:

inbreeding avoidance;
natal dispersal;
opportunity costs;
sex bias;
Seychelles warbler.

Abstract

In this study, we test whether patterns of territory inheritance, social mate choice and female-biased natal dispersal act as inbreeding avoidance mechanisms in the cooperatively breeding Seychelles warbler. Our results show that Seychelles warblers do not reduce the likelihood of inbreeding by avoiding related individuals as mates. The occurrence of natural and experimentally induced territory inheritance did not depend on whether the remaining breeder was a parent of the potential inheritor or an unrelated breeder. Furthermore, dispersing individuals were no less related to their eventual mates than expected given the pool of candidates they could mate with. The female bias in natal dispersal distance observed in the Seychelles warbler does not facilitate inbreeding avoidance because, contrary to our prediction, there was no sex difference in the clustering of related opposite sex breeders around the natal territories of dispersers. As a result, the chance of females mating with relatives was not reduced by their greater dispersal distance compared with that of males.

Introduction

Dispersal of individuals from their natal group to reproduce is common in most vertebrate taxa and generally the rate or distance of such natal dispersal is sex biased (Greenwood, 1980; Clarke *et al.*, 1997). Inbreeding avoidance has frequently been hypothesized to have contributed to the evolution of natal dispersal (e.g. Packer, 1979; Greenwood, 1980; Pusey, 1987). By leaving the natal area young may reduce the chance of eventually mating with a parent, while a sex bias in the rate or distance of dispersal is thought to result in the spatial separation of siblings. Although alternative processes, such as intra-sexual competition for mates (Dobson, 1982; Moore & Ali, 1984) may also play a role (Johnson & Gaines, 1990; Handley & Perrin, 2007), several field studies do suggest that natal dispersal is indeed an adaptation to inbreeding avoidance (Packer, 1979; Balcombe, 1989; Koenig *et al.*, 1998).

Correspondence: Cas Eikenaar, Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands.

Tel.: +31 50 3635928; fax: +31 50 3632148;
e-mail: c.eikenaar@rug.nl

There are, however, costs associated with dispersal, both in terms of survival (Johnson & Gaines, 1990) and reproduction. For example, the probability of an individual gaining a breeder position decreases with increasing dispersal distance from the natal territory (Stamps, 1987; Beletsky & Orians, 1993). Furthermore, territory inheritance does not necessarily lead to inbreeding, e.g. an opposite sex parent may be replaced by an unrelated individual at the time of territory inheritance (Woolfenden & Fitzpatrick, 1986; Koenig *et al.*, 1998). Therefore, if natal dispersal has evolved to avoid inbreeding then selection should also be expected to favour individuals that recognize when to disperse and when to stay; i.e. when a natal area breeder vacancy involves a closely related individual that they should avoid as a mate as opposed to an unrelated individual that they can mate with. Although many mate choice experiments have shown that individuals avoid mating with litter- or nestmates and siblings (reviewed in Pusey & Wolf, 1996), few field studies have provided evidence for inbreeding avoidance through mate choice within the natal territory. In the Florida scrub-jay (*Aphelocoma coerulescens*), territory inheritance was observed more often when the surviving breeder was a stepparent of the

nonbreeder heir rather than its natural parent (Woolfenden & Fitzpatrick, 1986; Balcombe, 1989). Moreover, we are unaware of field studies that have experimentally investigated whether young are more likely to inherit a territory with a stepparent than with a parent. If natal dispersal has evolved to avoid inbreeding then selection should also be expected to favour dispersers that subsequently choose unrelated individuals as mates. However, in many species, individuals that disperse from the natal site to breed often do not seem to reduce inbreeding through active mate choice (Keller & Arcese, 1998; Daniels & Walters, 2000; Richardson *et al.*, 2004; Van de Castele & Matthysen, 2006; Hansson *et al.*, 2007; but see Wheelright & Mauck, 1998; Wheelright *et al.*, 2006).

The evolution of sex-biased dispersal has received as much attention as dispersal itself, with many studies linking a sex bias in natal dispersal distance (NDD) to inbreeding avoidance (Greenwood, 1980; Pusey, 1987; Biek *et al.*, 2006; Vignieri, 2007). Although one sex may disperse further than the other, there is normally considerable overlap in NDD between the sexes (e.g. Woolfenden & Fitzpatrick, 1984; Koenig *et al.*, 2000). This implies that the separation of closely related opposite sex individuals through sex-biased dispersal is far from complete. Therefore, to determine if sex-biased natal dispersal functions to avoid inbreeding we need to know if the difference in NDD between the sexes is sufficient to reduce the chance of mating between close relatives. This is a major challenge, because it requires unbiased dispersal data and accurate knowledge of the spatial distribution of related individuals within the dispersal range (Van de Castele & Matthysen, 2006).

The population of Seychelles warbler (*Acrocephalus sechellensis*) on Cousin Island provides a unique opportunity to investigate the role of dispersal patterns in inbreeding avoidance for two reasons. First, the intense long-term monitoring of this small isolated population means that the natal dispersal histories of almost all individuals is known for many cohorts of individuals (Eikenaar *et al.*, 2008). Second, but perhaps more importantly, as off-island dispersal is virtually absent (Komdeur *et al.*, 2004a), the patterns of dispersal observed are not biased by a lack of data on individuals that disperse outside the area of observation. In this species, NDD is female biased, but distances overlap between the sexes (median NDD: males = 2 and females = 4 territory widths, Eikenaar *et al.*, 2008). Furthermore, there is evidence that close inbreeding occurs in this population (Richardson *et al.*, 2004; Brouwer *et al.*, 2007), which may have fitness effects. Finally, because the entire population has been genotyped using a suite of 30 previously isolated microsatellite loci (Richardson *et al.*, 2000; D.A. Dawson, unpublished results) relatedness values between dispersers and breeders can be estimated.

The aims of the current study are threefold. First, we assess if territory inheritance in the Seychelles warbler depends on the degree of relatedness between the

potential heir and the surviving breeder. This is carried out using both natural correlative data and a removal experiment in which nonbreeders were given the opportunity to inherit a breeder position by pairing up with either a parent or a stepparent. We predict territory inheritance to occur only with unrelated breeders.

Second, we assess if individuals that do disperse from their natal territory avoid related individuals as mates. A previous study on the Seychelles warblers that compared the relatedness of existing pairs with all potential random pairs across the entire population found no evidence for inbreeding avoidance through social or extra-pair mate choice (Richardson *et al.*, 2004). However, as most dispersers in this population settle relatively close to the natal territory (Eikenaar *et al.*, 2008), including all opposite sex breeders as candidate mates may not be realistic. In the current study, we limit the pool of candidate mates to those that were present within the distance that included 95% of observed NDDs. We also assess whether there is a relation between the distance an individual disperses and the number and pattern of closely related opposite sex breeders in adjacent territories. If natal dispersal is a direct facultative response to the avoidance of inbreeding, we expect individuals to disperse further when the natal territory is surrounded by individuals to which they are related. Such facultative avoidance does, however, rely on kin recognition. In the Seychelles warbler, there is evidence for kin recognition on the natal territory (Richardson *et al.*, 2003); so, the possibility that this extends across nearby territories is plausible.

Third, we assess whether the female bias in NDD contributes to inbreeding avoidance; specifically whether this dispersal bias is associated with a difference in the distribution of related individuals around the natal territories for each sex. For females, we expect clustering of closely related opposite sex breeders around their natal territories because their male siblings will previously have dispersed over short distances (Eikenaar *et al.*, 2008). For males, we expect little or no clustering of closely related opposite sex breeders around their natal territories because their female siblings will previously have dispersed over relatively long distances (Eikenaar *et al.*, 2008). If inbreeding is reduced by the greater female NDD, we expect that the chance of females mating with a close relative will be lower at the median female NDD than at the median male NDD. For males, we expect no difference between the median female and male NDD.

Methods

Study species and population

The Seychelles warbler is a passerine endemic to four small islands in the Seychelles. It is a facultative cooperative-breeding species that lives either in pairs, or in groups which normally consist of a primary pair and one or more offspring that have delayed dispersal and

remained in the natal territory as subordinates (Komdeur, 1992, 1994). Occasionally subordinates may also be previously dominant females that have been deposed (Richardson *et al.*, 2007). Some subordinates become helpers and assist in raising nondescendent kin, whereas other subordinates stay on the natal territory without engaging in helping behaviour (Komdeur, 1992; Richardson *et al.*, 2002, 2003). Males are equally likely to delay dispersal in their first year of life as females (Eikenaar *et al.*, 2007). They defend all-purpose territories year round (Komdeur, 1992) and breeder positions are generally acquired through the occupation of a vacancy that resulted from the death of a breeder, although some males become breeders by creating a new territory among the existing ones (Komdeur, 1992; C. Eikenaar, L. Brouwer and D.S. Richardson unpublished data.). Each group normally produces only a single egg every breeding season, but 20% of nests contain two or three eggs (Richardson *et al.*, 2001).

The present study was carried out on Cousin Island (29 ha) in the Seychelles. This population has been monitored intensively since 1985. Many of the birds have been caught (> 96% of birds since 1997; Richardson *et al.*, 2001) and individually colour ringed using a unique combination of three colour rings and a British Trust for Ornithology metal ring. Blood samples (approximately 25 μ L) were taken from captured birds by brachial venipuncture and stored in 100% ethanol at room temperature. Molecular sexing using the polymerase chain reaction (PCR) method devised by Griffiths *et al.* (1998) was used to confirm the sex of each individual.

The Cousin Island population has been relatively stable since 1982 with 105–120 territories (containing a total of 300–350 individuals) and, except for a barren rocky outcrop in the centre of the island, all habitat is occupied. Each territory borders, on average, five other territories. In most years since 1985, all territories were mapped in detail. For every colour-ringed individual, the status (primary or subordinate) and territory of residence were determined in each year during the peak breeding season (June to September), and in some years also during the minor breeding peak (December to January). The primary male and female were defined as the dominant, pair-bonded male and female in the territory. All other birds that were old enough to disperse (> 6 months old) but were still resident in the territory were defined as subordinates. During fieldwork periods, all territories were checked at least once every 2 weeks. As inter-island dispersal is extremely rare (0.1%, $n = 1924$, Komdeur *et al.*, 2004a) warblers that were missing from their territory and not found on other territories were assumed to have died.

Calculation of relatedness

We used the software program KINSHIP (Goodnight & Queller, 1999) to calculate individual pairwise related-

ness estimates (r) based on genotypic similarity at 30 microsatellite loci (Richardson *et al.*, 2000; D.A. Dawson unpublished data). Pairwise relatedness, which ranges from -1 to $+1$, is a measure of the extent to which two individuals have alleles that are identical by descent relative to allele frequencies in the entire population. A positive value signifies that two individuals are related, whereas values of zero or below indicate nonrelatives. In the 1997–1999 sample, mother–offspring relatedness for assigned offspring was normally distributed around a mean of 0.46 ± 0.15 SD (Kolmogorov–Smirnov $Z = 1.01$, $n = 130$, $P = 0.26$). To discriminate between closely (first-order relatives) and moderately (lower than first-order relatives) related individuals, we also calculated the distribution of second-order relatives (using half-siblings). Half-siblings' relatedness was normally distributed around a mean of 0.23 ± 0.19 SD (Kolmogorov–Smirnov $Z = 0.4$, $n = 128$, $P = 0.99$). Because the two distributions overlap, some closely related individuals could mistakenly be assigned as moderately related and vice versa. To minimize the number of incorrect assignments, we used the relatedness value $r = 0.35$ as the cut-off point between close and moderately related, because this point approximates the relatedness estimate where the normal distributions for mother–offspring and for half-siblings meet.

Territory inheritance

Since 1985, eight (five males and three females) of the 219 warblers (3.7%) for which the complete natal dispersal history is known inherited their natal territory. For these eight individuals, we estimated the degree of relatedness between them and their social mate in the newly inherited territory. We used genealogies and where possible also calculated the r between the individuals of the pairs that formed after territory inheritance.

In 2004, birds were caught on Cousin and transferred to Denis Island by Nature Seychelles as part of the long-term conservation effort to save the Seychelles warblers. We used this opportunity to perform a breeder removal experiment to test if territory inheritance depends on the degree of relatedness between the potentially inheriting subordinates and the remaining breeders. In 10 territories, we removed the primary breeder (five males and five females) that was the same sex as the subordinate(s) living in that territory. Each of the five territories in which the breeder female was removed contained a single female subordinate. Three territories in which the breeder male was removed contained a single male subordinate, whereas two territories held two male subordinates each, one of which was randomly excluded in the analysis. All subordinates were old enough to breed and could potentially inherit the breeder position in the territory by mating with the 'widowed' breeder. Genealogies indicated that in five territories the remaining

breeder was a (social) parent of the subordinate, whereas in five territories it was a (unrelated) breeder that had replaced a parent. Calculations of r between breeders and potential inheritors matched genealogies in all but one occasion. Excluding this exception, the mean r was 0.41 ± 0.12 when genealogy indicated a parent and 0.03 ± 0.08 when genealogy indicated a replacement. The exception was a 'widowed' breeder male whose 'daughter' was the result of extra-pair paternity, which is frequent in this species (40%, Richardson *et al.*, 2001). We assigned this male to the parent group because social, not genetic, parentage represents the offspring's perception of who their parents are (Richardson *et al.*, 2003; Komdeur *et al.*, 2004b). Therefore, five subordinates had the opportunity to mate with a (perceived) parent and five had the opportunity to mate with an apparently unrelated replacement.

Mate choice of dispersers

All dispersal data are based on individuals that were caught and ringed for the first time while still living on their natal territory. These individuals were either ringed in the nest or caught within 6 months of fledging while still reliant on their parents (on Cousin young never disperse before 6 months of age, Komdeur, 1996; C. Eikenaar, unpublished work). NDD was defined as the minimal number of territories an individual traversed from its natal territory to reach its breeding territory, measured in a straight line.

For individuals that fledged between 1997 and 1999 – three years for which we had exceptionally accurate data on the reproductive output of all individuals in all territories (Richardson *et al.*, 2002) – and had a known natal dispersal history, we assessed whether they were less related to their chosen mates than could be expected from random mating. We expressed expected values in two ways: (a) as the average r between dispersers and all their candidate mates; and (b) as the proportions of closely or moderately related pairs that would have resulted from all pairings between dispersers and their candidate mates. We defined the pool of candidate mates as all opposite sex primary breeders that were present outside the natal territory but within the distance that included 95% of observed NDDs. This was estimated as seven territory widths for males and eight territory widths for females. The two dispersers that paired with an unringed breeder were excluded from the analyses.

Structuring of relatedness across the landscape

We calculated r between each disperser (fledged between 1997 and 1999) and all the opposite sex primary breeders present in the population in the year the disperser settled as a primary breeder. These values were used to construct the relatedness landscape that individuals faced in the year they dispersed. We expressed this relatedness

landscape in two different ways. First, we expressed it as the averages of the r between each disperser and all the opposite sex primary breeders at each potential NDD, i.e. average r of all opposite sex primary breeders in territories adjacent to the natal territory, two territories distant from the natal territory, etc. Second, we expressed it as the proportions of opposite sex primary breeders that were closely ($r \geq 0.35$) or moderately ($0.10 < r < 0.35$) related to the disperser at each potential NDD. Relatedness landscapes were calculated separately for male and female dispersers. Some birds dispersed from the centre of the population and, consequently, had a lower maximum potential NDD than birds that dispersed from the periphery of the population. To avoid bias due to decreasing sample sizes at the higher end of potential NDDs, calculations for the relatedness landscapes were limited to the smallest maximum potential NDD in the data set, which was seven territory widths. In the rare instances that either two brothers or two sisters originating from the same territory settled in the same year, only one randomly selected individual was included in the calculation of relatedness landscapes. Inclusion of both individuals could result in pseudo-replication because: (a) they are closely related; and (b) for each disperser we calculated its average relatedness to all opposite sex breeders at each dispersal distance, in the year the disperser settled. In other words, two brothers or two sisters from one territory would affect the calculated spatial distribution of related individuals across the population more than a single individual would.

Data analyses

Transformations and nonparametric tests were used where appropriate. Proportional data were arcsine square root transformed prior to analyses. All tests were performed using SPSS 14.0 (SPSS Inc. 1999) and were two tailed. Statistical significance was set at $P < 0.05$. Because the sample was small, we used Fisher's exact test to assess if experimental territory inheritance depended on the degree of relatedness between the potential inheritor and the surviving breeder. For all tests, sample mean values and the 95% confidence interval (CI) around the difference of the mean values are presented.

Results

Territory inheritance

Of the eight instances of natural territory inheritance, five subordinates mated with a (social) parent and three mated with a breeder that had replaced a parent. Relatedness values could be calculated for three of the five parent-offspring pairs and were 0.47, 0.43 and –0.06. This last r was low, because, although the breeder male mated with his apparent 'daughter', this 'daughter' was actually the result of extra-pair paternity. Relatedness

values could be calculated for two of the three instances of inheritance with a replacement breeder and were 0.05 and -0.06 . This suggests that there was no inbreeding avoidance through mate choice within the natal territory.

The territory inheritance experiment confirmed the absence of inbreeding avoidance through differential territory inheritance; inheritance did not occur more often with a stepparent than with a parent (Fisher's exact test: $P = 0.52$, $n = 10$). Of the five subordinates that had the opportunity to inherit the territory and mate with a replacement breeder only one did so, while three of the five subordinates that had the opportunity to inherit the territory and mate with a parent did so.

Mate choice of dispersers

Dispersing subordinates did not seem to avoid inbreeding through mate choice. The relatedness of dispersers to their chosen mates actually was higher than the average relatedness to candidate mates (0.06 and -0.01 respectively; CI 0.02–0.12; paired samples t -test: $t_{67} = 2.72$, $P = 0.01$). Similarly, the proportion of mates that was closely related to the dispersers was higher for chosen than for candidate mates (0.08 and 0.03 respectively; CI 0.01–0.15; chi-square test: $\chi_1^2 = 4.68$, $P = 0.03$, $n = 68$). The proportion of mates that was moderately related to the dispersers was not different between chosen and candidate mates (0.29 and 0.26 respectively; CI -0.06 to 0.16; chi-square test: $\chi_1^2 = 0.57$, $P = 0.45$, $n = 68$).

The distance that subordinates dispersed was not correlated with the proportion of related opposite sex breeders present in territories adjacent to the natal one (Fig. 1, Spearman rank correlation: closely related: $\rho = 0.09$, $P = 0.47$, $n = 70$; moderately related: $\rho = -0.04$, $P = 0.74$, $n = 70$). Furthermore, the proportion of related opposite sex breeders present in territories adjacent to the natal one did not differ between dispersers that settled in their natal or in an adjacent territory and dispersers that settled further (closely related: 0.08 and 0.1 respectively; CI -0.1 to 0.06; Mann–Whitney U -test: $Z = -0.85$, $P = 0.39$, $n = 70$; moderately related: 0.27 and 0.26 respectively; CI -0.1 to 0.12; $Z = -0.01$, $P = 0.99$, $n = 70$). These results on dispersal distance were similar when tested separately for the sexes.

Dispersal and relatedness landscape

There was little apparent clustering of related opposite sex breeders around the natal territories of dispersers (Figs 2 and 3), except for a slight elevation in the proportion of closely related opposite sex breeders in territories very close to the natal territories of dispersers. This elevation seemed most pronounced for female dispersers (Fig. 2a). However, the proportion of closely related opposite sex breeders in adjacent territories was not different between females and males (0.12 and 0.07

respectively; CI -0.02 to 0.12; Mann–Whitney U -test, $Z = -1.29$, $P = 0.20$, $n = 70$). Furthermore, the proportion of closely related opposite sex breeders in territories within the median male NDD (two territory widths) was not different between females and males (0.08 and 0.05 respectively; CI -0.01 to 0.07; Mann–Whitney U -test, $Z = -1.02$, $P = 0.31$, $n = 70$). Therefore, when dispersing to territories very close to the natal territory, females do not have a higher chance of pairing with a closely related individual than males.

For female dispersers, there was no difference in the proportion of related male breeders that would be encountered at the median female NDD (four territory widths) and median male NDD (closely related: 0.04 and 0.05 respectively; CI -0.05 to 0.03; Wilcoxon signed ranks test: $Z = -0.41$, $P = 0.68$, $n = 37$; moderately related: 0.23 and 0.3 respectively; CI -0.15 to 0.01; paired samples t -test: $t_{36} = 1.54$, $P = 0.13$). Nor was there a difference in the mean level of r between female dispersers and all male breeders at the median male and median female NDD (0.02 and 0.01 respectively; CI -0.03 to 0.06; paired samples t -test: $t_{36} = 0.67$, $P = 0.50$). For male dispersers, there was no difference in the proportion of related primary female breeders at the median female and median male NDD (closely related: 0.02 and 0.03 respectively; CI -0.04 to 0.02; Wilcoxon signed ranks test: $Z = -0.77$, $P = 0.44$, $n = 33$; moderately related: 0.29 and 0.27 respectively; CI -0.08 to 0.12; paired samples t -test: $t_{32} = -0.56$, $P = 0.58$). Nor was there a difference in the mean level of r between male dispersers and all primary female breeders at the median female and median male NDD (0.001 and -0.001 respectively; CI -0.04 to 0.04; paired samples t -test: $t_{32} = -0.12$, $P = 0.91$).

Discussion

Inbreeding avoidance through mate choice

Our results indicate that Seychelles warblers do not appear to reduce inbreeding either through differential territory inheritance, social mate choice or sex-biased dispersal. This suggests that in this species, in its current environment, natal dispersal does not facilitate inbreeding avoidance. First, the occurrence of territory inheritance did not depend on whether or not the opposite sex breeder that the heir would have to pair up with was a parent or an unrelated replacement. This contrasts with findings in other cooperative breeders in which dispersal has been shown to be associated with inbreeding avoidance. In the Florida scrub-jay, territory inheritance was observed more often when the surviving breeder was a stepparent of the nonbreeder heir rather than its natural parent (Woolfenden & Fitzpatrick, 1986; Balcombe, 1989). In the acorn woodpecker (*Melanerpes formicivorus*), young were more likely to disperse following the death of a breeder of the same sex, rather than the opposite sex

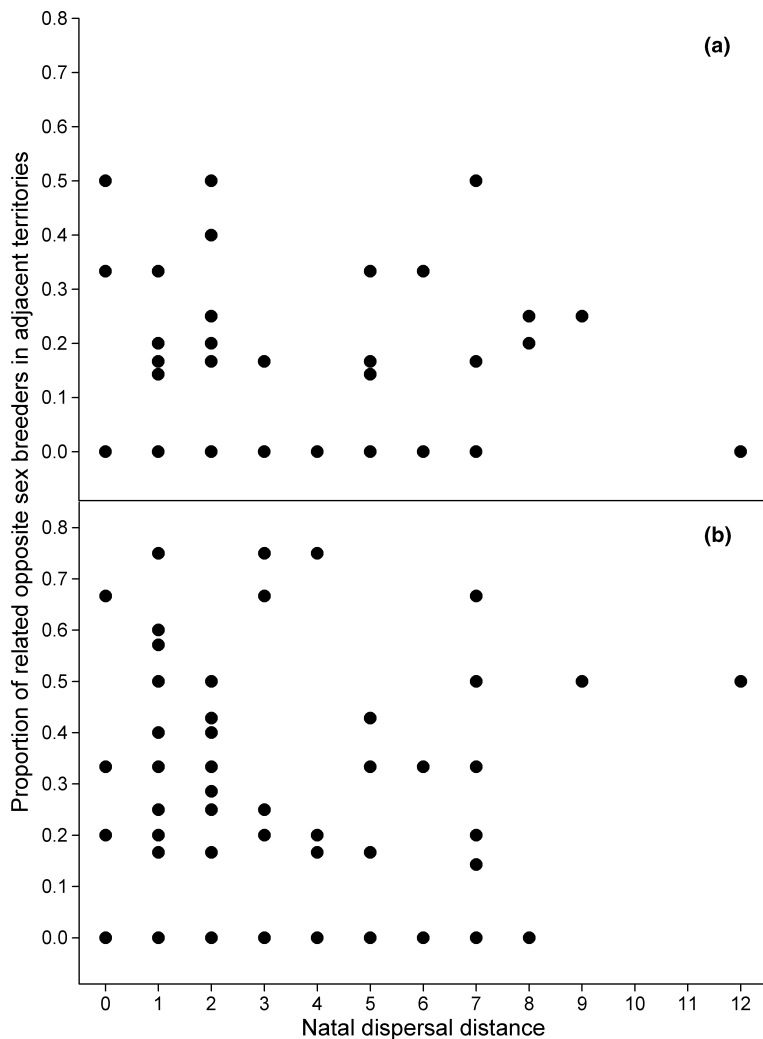


Fig. 1 The relationship between observed natal dispersal distances and the proportion of opposite sex breeders in adjacent territories that were: (a) closely and (b) moderately related to the disperser ($n = 70$).

(Koenig *et al.*, 1998). Second, in the Seychelles warbler, the chosen mates of individuals that did disperse were more, instead of less, related to them than the average relatedness to all candidate mates. This may have resulted from a combination of our definition of the pool of candidate mates and the slight elevation in the proportion of closely related opposite sex breeders in territories very close to the natal territories of dispersers (Figs 2 and 3). Many dispersers settle very close to the natal territory (in the 1997–1999 sample, 26% of dispersers settled in a territory adjacent to their natal one), where the chances of mating with a close relative are the highest. The pool of candidate mates was defined based on a certain dispersal distance. The smaller this distance, the higher the proportion of closely related mates will be in the pool of candidates. Indeed, when the pool of candidate mates was restricted to the median NDD (and thus smaller than when restricted to include candidate mates within 95% of observed dispersal

distances) dispersers were not more related to their chosen mate than expected by chance (paired samples t -test: $t_{67} = 1.89$, $P = 0.06$). One can, however, debate if such a restriction is realistic, as half of the chosen mates then lived outside the range of the pool of candidate mates. Alternatively this observation could be the result of a preference of dispersers for related individuals as mates, however, additional mate choice experiments are required to test this hypothesis. Likewise, in many other species individuals dispersing from the natal site to breed do not seem to be able to reduce inbreeding through active mate choice (Keller & Arcese, 1998; Daniels & Walters, 2000; Duarte *et al.*, 2003; Foerster *et al.*, 2006; Van de Castele & Matthysen, 2006; Hansson *et al.*, 2007). One notable exception is Savannah sparrows (*Passerculus sandwichensis*), in which incestuous pairings are almost absent and dispersers settle further from their siblings than expected by chance (Wheelright & Mauck, 1998; Wheelright *et al.*, 2006). Male Savannah sparrows

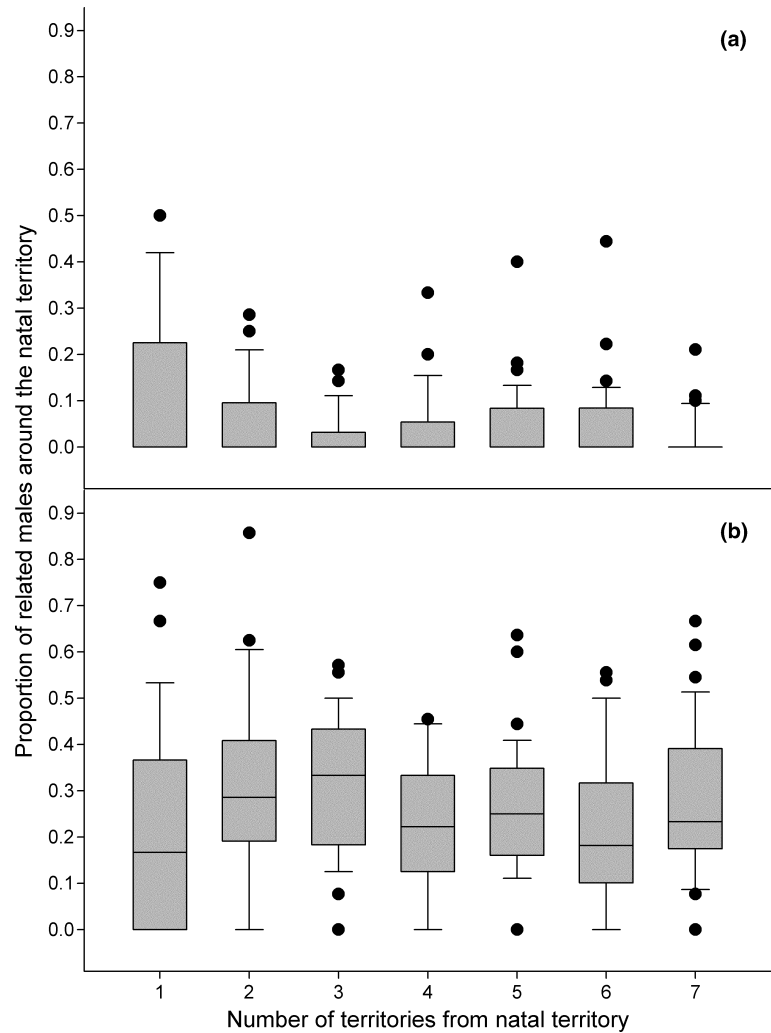


Fig. 2 Box plots of the proportion of (a) closely ($r \geq 0.35$) and (b) moderately ($0.1 < r < 0.35$) related males around the natal territories of dispersing Seychelles warbler females, categorized by the number of territories away from the natal territory ($n = 37$). Outliers are indicated by solid circles. Median dispersal distances were two territory widths for males and four territory widths for females.

often sing immediately after feeding their fledglings. Possibly females learn and recognize their fathers' song and if song characteristics are inherited, females may be able to avoid pairing with male siblings, even when raised in different years (Wheelright & Mauck, 1998). As Seychelles warblers do not sing at the nest when provisioning (C. Eikenaar, personal observations), it seems unlikely that the young of this species are imprinted on their fathers' song.

The lack of inbreeding avoidance through active mate choice implies that inbreeding must occur in the Cousin population of Seychelles warblers. Indeed, a previous study on the same population estimated that 5% of nestlings were the result of inbreeding between first-order relatives (Richardson *et al.*, 2004). It was suggested that part of such pairings resulted from subordinate females mating and reproducing with their father on their natal territories (Richardson *et al.*, 2001, 2002, 2004). The current study revealed that inbreeding may

also result from territory inheritance and from the failure of dispersers to select unrelated individuals as mates. The lack of inbreeding avoidance also suggests that selection against inbreeding is, at least at present, not strong in the Seychelles warbler. Indeed previous studies on the Seychelles warbler showed that an individual's survival was not correlated with its own heterozygosity (Richardson *et al.*, 2004; Brouwer *et al.*, 2007). Low maternal heterozygosity was, however, associated with reduced offspring survival (Richardson *et al.*, 2004; Brouwer *et al.*, 2007), indicating that there is weak inbreeding depression.

A lack of inbreeding avoidance has also been observed in several well-studied populations where inbreeding depression is considerable (e.g. song sparrow (*Melospiza melodia*), Keller & Arcese, 1998; red-cockaded woodpecker (*Picoides borealis*), Daniels & Walters, 2000; great tit (*Parus major*), Bulmer, 1973; Szulkin *et al.*, 2007). This lack of avoidance may result from the fact that, in some

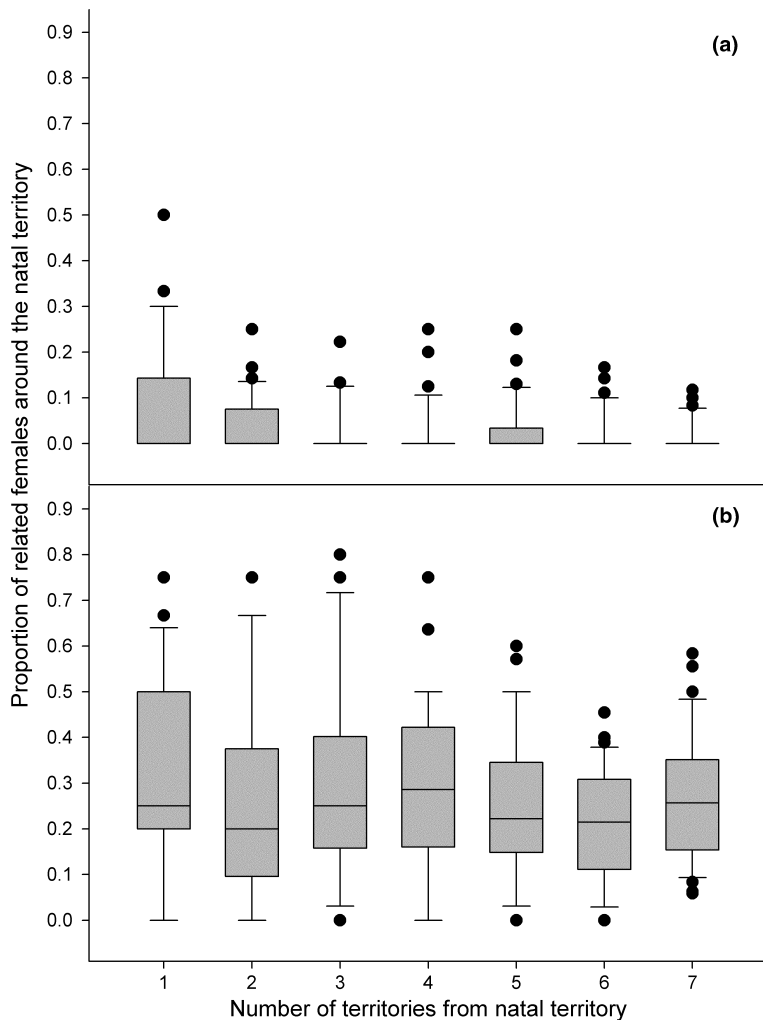


Fig. 3 Box plots of the proportion of (a) closely ($r \geq 0.35$) and (b) moderately ($0.1 < r < 0.35$) related females around the natal territories of dispersing Seychelles warbler males, categorized by the number of territories away from the natal territory ($n = 33$). Outliers are indicated by solid circles. Median dispersal distances were two territory widths for males and four territory widths for females.

situations, inbreeding avoidance may be more costly than inbreeding depression (Waser *et al.*, 1986). For example, when mating opportunities are rare, individuals may miss valuable chances to reproduce if they attempt to avoid mating with kin. In the following section, we attempt to roughly estimate these opportunity costs for young Seychelles warblers. Most prospective breeders (≥ 6 months old) delay dispersal and wait for a nearby breeder position to become available as a result of a territory owner dying (Komdeur, 1992; C. Eikenaar, L. Brouwer and D.S. Richardson, unpublished data). There is, however, strong competition for vacant breeder positions, because each year there is a large surplus of prospective breeders in the population (1995–2004: mean \pm SD 77 ± 18 ; C. Eikenaar, unpublished results). The population consists of on average 112 territories (and thus 224 dominant breeders) each year and annual adult mortality rate is equally low for both sexes (16%, Brouwer *et al.*, 2006). This means that on average 36 breeder positions (224×0.16) become

available each year. Therefore, each year there are, on average, just over two prospective breeders for each breeder position that becomes available. For the sake of simplicity, we assume that: (a) vacancies open at a regular rate during the year; and (b) prospective breeders that do not occupy a vacancy in the first year, always occupy a vacancy in the next year. Consequently, one of the two prospective breeders will occupy a vacancy somewhere between 0 and 12 months after it started searching for breeder vacancies, whereas the other will occupy a vacancy somewhere between 13 and 24 months after it started searching. This means that, on average, it will take 12 months from the moment a prospective breeder starts searching for breeder vacancies until it occupies one. If all prospective breeders start searching when 6 months old then they would on average be 18 months old when they first occupy a vacancy. However, if a prospective breeder forsakes a vacancy to avoid inbreeding, it would take on average another 12 months until the next opportunity arrives. In

the Seychelles warbler the average lifespan of birds surviving the first year is 4 years (Brouwer *et al.*, 2007). Consequently, a prospective breeder that takes the first breeding opportunity that arises will have on average 3.5 years to reproduce, whereas one that forsakes this opportunity (and therefore must wait another 12 months) will have only 2.5 years left in which to reproduce. Forsaking just one opportunity to occupy a breeder vacancy may, therefore, reduce the reproductive lifespan of an individual by nearly a third (2.5 year vs. 3.5 year). As inbreeding depression appears to be very limited in this population (Richardson *et al.*, 2004; Brouwer *et al.*, 2007), such relatively high avoidance costs would probably prevent the evolution of inbreeding avoidance in the Seychelles warbler.

In our study population, dispersal distances are restricted by the boundaries of the small (26 ha) island (Komdeur *et al.*, 2004a). Therefore, the costs of inbreeding avoidance, in terms of forsaking opportunities to occupy a breeder vacancy, are probably increased when compared with study systems where dispersal distances (and therefore mating opportunities) are not so constrained by physical boundaries. Such differences in the cost of forsaking breeding vacancies may have contributed to the observation that, as opposed to Seychelles warblers, other bird species such as the Florida scrub-jay and acorn woodpecker do avoid pairing with a parent on the natal territory (Woolfenden & Fitzpatrick, 1986; Balcombe, 1989; Koenig *et al.*, 1998).

Inbreeding avoidance through sex-biased dispersal

Our results indicate that the female bias in NDD observed in the Cousin population (Eikenaar *et al.*, 2008) does not contribute to inbreeding avoidance. Contrary to our prediction, there was no difference between the sexes in the proportion of related opposite sex breeders at the median male and female NDD. Furthermore, the chance of mating with a close relative when dispersing within the median male NDD was not higher for females than for males. This implies that to avoid inbreeding females would not need to disperse beyond the median male NDD. Inconsistencies between observed patterns of dispersal and the relatedness structure within a population have been observed before (e.g. Biek *et al.*, 2006) and have been hypothesized to result from inconspicuous components of dispersal or mating behaviour (e.g. cryptic migration, extra-pair paternity and polyandry, Winters & Waser, 2003; Vignieri, 2007). The dispersal data in our study are virtually unbiased (due to the complete sampling of the population and the lack of migration); however, the high levels of extra-pair paternity in the Cousin population (40% Richardson *et al.*, 2001) will have reduced dramatically the degree of relatedness between siblings. Because males disperse shorter distances than females (Eikenaar *et al.*, 2008) for female dispersers, we expected stronger clustering of

related opposite sex breeders around their natal territories than for male dispersers. The low degree of relatedness between siblings will have weakened this sex difference. A further explanation for the absence of a clear sex difference in clustering of related opposite sex breeders may be that for most dispersing individuals very few opposite sex siblings would have previously recruited into the breeding population. This is a consequence of high adult survival probabilities (84%, Brouwer *et al.*, 2006) which means that few breeder vacancies open each year and only a small fraction of the young will be able to settle as a breeder.

But why do Seychelles warbler females disperse further than males if it does not reduce inbreeding? Other main evolutionary models for sex-biased natal dispersal (local mate and resource competition, Greenwood, 1980; Dobson, 1982) also seem inappropriate explanations for the female-biased NDD in the Seychelles warbler (Eikenaar *et al.*, 2008). Is it possible that this bias is merely a phylogenetic relic which is, at present, of no adaptive significance? In passerines, females generally disperse further than males (Greenwood, 1980; Clarke *et al.*, 1997). However, in the closely related great reed warbler (*Acrocephalus arundinaceus*) a capture–recapture study did not find a sex bias in NDD (Hansson *et al.*, 2002). Unfortunately, with data on NDD in other *Acrocephalus* species lacking, the idea that the female bias in NDD is a phylogenetic relic remains speculative. Nevertheless, if the female-biased NDD is indeed of no adaptive significance, selection against this bias cannot be very strong.

Conclusions

Our results show that Seychelles warblers do not avoid inbreeding through active mate choice on the natal territory or when dispersing and that the female bias in NDD does not contribute to inbreeding avoidance. We argue that the combination of relatively mild inbreeding depression and the high costs of forsaking mating opportunities counteract inbreeding avoidance in the Seychelles warbler.

Acknowledgments

Nature Seychelles kindly allowed us to work on Cousin Island, conducted the translocation and provided accommodation and facilities during the stay. The Department of Environment and the Seychelles Bureau of Standards gave permission for fieldwork and sampling. We thank everyone that helped in the field since 1985, and K. Bouwman and two anonymous referees for constructive comments on the manuscript. This work was supported by a Marie Curie Fellowship (HPMF-CT-2000-01074) and a NERC postdoctoral fellowship (NER/I/S/2002/00712) awarded to David S. Richardson, by grants from the National Environmental Research Council to Terry Burke and Jan Komdeur (GR3/11154),

the Large Australian Research Council (A19802459) and the Netherlands Organisation for Scientific Research (NWO-VICI, 86503003), both allocated to Jan Komdeur.

References

- Balcombe, J.P. 1989. Non-breeder asymmetry in Florida scrub jays. *Evol. Ecol.* **3**: 77–79.
- Beletsky, L.D. & Orians, G.H. 1993. Factors affecting which male red-winged blackbirds acquire territories. *Condor* **95**: 782–791.
- Biek, R., Akamine, N., Schwartz, M.K., Ruth, T.K., Murphy, K.M. & Poss, M. 2006. Genetic consequences of sex-biased dispersal in a solitary carnivore: Yellowstone cougars. *Biol. Lett.* **2**: 312–315.
- Brouwer, L., Richardson, D.S., Eikenaar, C. & Komdeur, J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *J. Anim. Ecol.* **75**: 1321–1329.
- Brouwer, L., Komdeur, J. & Richardson, D.S. 2007. Heterozygosity–fitness correlations in a bottlenecked island species; a case study on the Seychelles warbler. *Mol. Ecol.* **16**: 3134–3144.
- Bulmer, M.G. 1973. Inbreeding in the great tit. *Heredity* **30**: 313–325.
- Clarke, A.L., Sæther, B.E. & Røskaft, E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* **79**: 429–438.
- Daniels, S.J. & Walters, J.R. 2000. Inbreeding depression and its effects on natal dispersal in red-cockaded woodpeckers. *Condor* **102**: 482–491.
- Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**: 1183–1192.
- Duarte, L.C., Bouteiller, C., Fontanillas, P., Petit, E. & Perrin, N. 2003. Inbreeding in the greater white-toothed shrew, *Crocidura russula*. *Evolution* **57**: 638–645.
- Eikenaar, C., Richardson, D.S., Brouwer, L. & Komdeur, J. 2007. Parent presence, delayed dispersal and territory acquisition in the Seychelles warbler. *Behav. Ecol.* **18**: 874–879.
- Eikenaar, C., Richardson, D.S., Brouwer, L. & Komdeur, J. 2008. Sex biased dispersal in a closed, saturated population of Seychelles warblers. *J. Avian Biol.* **39**: 73–80.
- Foerster, K., Valcu, M., Johnson, A. & Kempenaers, B. 2006. A spatial genetic structure and effects of relatedness on mate choice in a wild bird population. *Mol. Ecol.* **15**: 4555–4567.
- Goodnight, K.F. & Queller, D.C. 1999. Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* **8**: 1231–1234.
- Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.G.J. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7**: 1071–1075.
- Handley, L.J.L. & Perrin, N. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* **16**: 1559–1578.
- Hansson, B., Bensch, S., Hasselquist, D. & Nielsen, B. 2002. Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia* **130**: 536–542.
- Hansson, B., Jack, L., Christians, J.K., Pemberton, J.M., Åkesson, M., Westerdahl, H., Bensch, S. & Hasselquist, D. 2007. No evidence for inbreeding avoidance in a great reed warbler population. *Behav. Ecol.* **18**: 157–164.
- Johnson, M.L. & Gaines, M.S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu. Rev. Ecol. Syst.* **21**: 449–480.
- Keller, L.F. & Arcese, P. 1998. No evidence for inbreeding avoidance in a natural population of song sparrows. *Am. Nat.* **152**: 380–392.
- Koenig, W.D., Haydock, J. & Stanback, M.T. 1998. Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. *Am. Nat.* **151**: 243–255.
- Koenig, W.D., Hooge, P.N., Stanback, M.T. & Haydock, J. 2000. Natal dispersal in the cooperatively breeding acorn woodpecker. *Condor* **102**: 492–502.
- Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**: 493–495.
- Komdeur, J. 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behav. Ecol. Sociobiol.* **34**: 175–186.
- Komdeur, J. 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. *Proc. R. Soc. Lond. B* **263**: 661–666.
- Komdeur, J., Piersma, T., Kraaijeveld, K., Kraaijeveld-Smit, F. & Richardson, D.S. 2004a. Why Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there? *Proc. R. Soc. Lond. B* **146**: 298–302.
- Komdeur, J., Richardson, D.S. & Burke, T. 2004b. Experimental evidence that kin discrimination in the Seychelles warbler is based on association and not on genetic relatedness. *Proc. R. Soc. Lond. B* **271**: 963–969.
- Moore, J. & Ali, R. 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.* **32**: 94–112.
- Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* **27**: 1–36.
- Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *TREE* **2**: 295–299.
- Pusey, A.E. & Wolf, M. 1996. Inbreeding avoidance in animals. *TREE* **11**: 201–206.
- Richardson, D.S., Jury, F.L., Dawson, D.A., Salgueiro, P., Komdeur, J. & Burke, T. 2000. Fifty Seychelles warbler (*Acrocephalus sechellensis*) microsatellite loci polymorphic in Sylviidae species and their cross-species amplification in other passerine birds. *Mol. Ecol.* **9**: 2226–2231.
- Richardson, D.S., Jury, F.L., Blaakmeer, K., Komdeur, J. & Burke, T. 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Mol. Ecol.* **10**: 2263–2273.
- Richardson, D.S., Burke, T. & Komdeur, J. 2002. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. *Evolution* **56**: 2313–2321.
- Richardson, D.S., Burke, T. & Komdeur, J. 2003. Sex-specific associative learning cues and inclusive fitness benefits in the Seychelles warbler. *J. Evol. Biol.* **16**: 854–861.
- Richardson, D.S., Komdeur, J. & Burke, T. 2004. Inbreeding in the Seychelles warbler: environment-dependent maternal effects. *Evolution* **58**: 2037–2048.
- Richardson, D.S., Burke, T. & Komdeur, J. 2007. Grandparent helpers: the adaptive significance of older, postdominant helpers in the Seychelles warbler. *Evolution* **61**: 2790–2800.
- SPSS Inc. 1999. *SPSS* Vers. 14.0. SPSS Inc., Chicago, IL.

- Stamps, J.A. 1987. The effect of familiarity with a neighborhood on territory acquisition. *Behav. Ecol. Sociobiol.* **21**: 273–277.
- Szulkin, M., Garant, D., McCleery, R.H. & Sheldon, B.C. 2007. Inbreeding depression along a life-history continuum in the great tit. *J. Evol. Biol.* **20**: 1531–1543.
- Van de Castele, T. & Matthysen, E. 2006. Natal dispersal and parental escorting predict relatedness between mates in a passerine bird. *Mol. Ecol.* **15**: 2557–2565.
- Vignieri, S.N. 2007. Cryptic behaviours, inverse genetic landscapes, and spatial avoidance of inbreeding in the Pacific jumping mouse. *Mol. Ecol.* **16**: 853–866.
- Waser, P.M., Austad, S.N. & Keane, B. 1986. When should animals tolerate inbreeding? *Am. Nat.* **128**: 529–537.
- Wheelright, N.T. & Mauck, R.A. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah sparrows. *Ecology* **79**: 755–767.
- Wheelright, N.T., Freeman-Gallant, C.R. & Mauck, R.A. 2006. Asymmetrical incest avoidance in the choice of social and genetic mates. *Anim. Behav.* **71**: 631–639.
- Winters, J.B. & Waser, P.M. 2003. Gene dispersal and outbreeding in a philopatric mammal. *Mol. Ecol.* **12**: 2251–2259.
- Woolfenden, G.E. & Fitzpatrick, J.W. 1984. Dispersal. In: *The Florida Scrub-jay: Demography of a Cooperative-breeding Bird* (G.E. Woolfenden and J.W. Fitzpatrick, eds), pp. 137–179. Princeton University Press, Princeton, NJ.
- Woolfenden, G.E. & Fitzpatrick, J.W. 1986. Sexual asymmetries in the life history of the Florida scrub jay. In: *Ecological Aspects of Social Evolution: Birds and Mammals* (D.I. Rubenstein & R.W. Wrangham, eds), pp. 87–107. Princeton University Press, Princeton, NJ.

Received 16 November 2007; revised 14 February 2008; accepted 21 February 2008